The role of head movements in the discrimination of 2D shape by blind echolocation experts

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Abstract

Similar to certain bats and dolphins, some blind humans can use sound echoes to perceive their silent surroundings. By producing an auditory signal (e.g. a mouth click) and listening to the returning echoes, these individuals can obtain information about their environment, such as the size, distance, and density of objects. Past research has also hinted at the possibility that blind individuals may be able to use echolocation to gather information about 2D surface shape, with definite results pending. Thus, here we investigated people's ability to use echolocation to identify the 2D shape (contour) of objects. We also investigated the role played by head movements, i.e. exploratory movements of the head while echolocating, because anecdotal evidence suggests that head movements might be beneficial for shape identification. To this end we compared the performance of six expert echolocators to that of ten blind non-echolocators and ten blindfolded sighted controls in a shape identification task with and without head movements. We found that expert echolocators could use echoes to determine the shapes of the objects with exceptional accuracy when they were allowed to make head movements, but that their performance dropped to chance level when they had to remain still. Neither blind nor blindfolded sighted controls performed above chance, regardless of head movements. Our results show not only that experts can use echolocation to successfully identify 2D shape, but also that head movements made while echolocating are necessary for correct identification of 2D shape.

Introduction

It is well known that some animals use self-generated sounds to perceive their surroundings via reflected sound waves, or echoes. Echolocation can be used in environments not conducive to vision, thereby allowing animals to navigate and forage even in complete darkness. Similarly, some blind humans have developed the ability to use echoes from self-produced sounds to perceive their silent surroundings. For example, blind echolocators can perceive information such as the size, shape, distance, motion, and material properties of silent objects (Arnott, Thaler, Milne, Kish, & Goodale, 2013; Kellogg, 1962; Rice, 1967; Rice, 1969; Rice & Feinstein, 1965; Rice, Feinstein, & Schusterman, 1965; Schenkman & Nilsson, 2010; Stoffregen & Pittenger, 1995; Teng, Puri, & Whitney, 2011; Teng & Whitney, 2011; Thaler, Arnott, & Goodale, 2011; Thaler, Milne, Arnott, Kish, & Goodale, 2013). In this way, then, echolocation could be considered a crude substitute for vision, allowing blind humans to perceive aspects of their environment that would otherwise go undetected.

Although our knowledge of echolocating animals such as dolphins and some species of bats is quite extensive (for example, see Harley, Putman, & Roitblat, 2003; Schnitzler & Kalko, 2001; Thomas, Moss, & Vater, 2004), comparably little research has been dedicated to understanding the use of echolocation by humans. In the 1940s, it was determined that blind individuals' ability to avoid obstacles and sense the presence of objects was not due to 'facial vision', but to the use of active auditory perception (Ammons, Worchel, & Dallenbach, 1953; Cotzin & Dallenbach, 1950; Supa, Cotzin, and Dallenbach, 1944). Following this discovery, a series of behavioural investigations of echolocation revealed the ability of blind echolocators to detect the presence of objects and also to comment on object features such as size, distance, and material properties (Kellogg, 1962; Rice, 1967; Rice, et al. 1965; Schenkman & Nilsson, 2010; Schörnich, et al. 2013; Teng et al., 2011). Studies have even provided evidence that sighted individuals can learn to echolocate as well (Teng & Whitney, 2011; Ammons et al., 1953).

Although human echolocation is receiving increasing attention in the literature, a clear understanding of the ability of blind echolocators to discern 2D shape is lacking. The perception of shape is likely important to a blind echolocator, for example during navigation where landmark identification and obstacle avoidance are critical. In 1967, Rice reported preliminary results of a 2D shape discrimination task which suggested that blind echolocators could distinguish between a circle, square, and triangle, but he never followed-up on these initial observations. Later, Hausfeld, Power, Gorta, and Harris (1982) showed that untrained sighted individuals could learn to discriminate simple shapes using echoes, and that a blind participant performed within the range of these sighted individuals. Furthermore, we know from the literature that echolocating bats can perceive the shape of objects from echoes and can use this information to discriminate between food and non-food objects (Simmons & Chen, 1989). Thus, it is reasonable to believe that blind expert echolocators can determine the shape of objects using echoes. What remains unclear in the literature, though, is how the use of movement affects shape identification. We know anecdotally that when expert echolocators are naturally using echolocation they typically make many movements with their head. In fact, almost all of the studies on echolocation from the last century mentioned that their echolocating subjects used head movements that seemed to aid in performance on the tasks, but no research has been done to follow up on these reports. In the context of 2D shape perception, head movements are likely to be useful for resolving the 2D shape of an object, for example by acoustically 'tracing the contour' of an object.

In sum, based on the evidence to date, the aim of the current study was two-fold: (1) to determine if blind expert echolocators can use echolocation to identify 2D shapes and (2) to determine if this behaviour is affected by imposing constraints on their head movements. We found that expert echolocators were remarkably accurate at identifying shapes when they were allowed to freely move and explore the objects as they would naturally; when they were required to remain still, however, their performance declined dramatically. The results of the current work contribute to our understanding of the applications of echolocation and show that head movement is crucial to successful object identification (at least in the case of 2D shape perception).

Methods

Participants

A total of 26 participants were recruited to participate in a shape identification experiment at The University of Western Ontario (London, Ontario, Canada). All testing procedures were approved by the University ethics board and participants gave written informed consent prior to testing. Participants were drawn from three different groups: blind expert echolocators (EE) (reported everyday use of active echolocation and extensive experience with the technique), blind controls (BC) (reported little to no use of active echolocation techniques), and blindfolded sighted controls (SC) (reported normal or corrected-to-normal vision and no experience with echolocation techniques). Blind participants who reported any residual vision (for example, bright light detection) were also blindfolded. All participants reported to have normal hearing and no history of hearing difficulties. See Table 1 for participant details.

It is important to note that blind and blindfolded sighted controls received no echolocation training prior to participating in the experiment. It is clear from previous research that sighted individuals can learn to use echoes (Teng & Whitney, 2011) and, of course, blind individuals can be trained as well. The purpose of the control participants in the current study, however, was to control for performance that could be attributed to factors other than echolocation expertise (super-sensitivity to echoes as a simple consequence of blindness, ambient sounds, sounds from the movements of the experimenter, etc.). The mouth-click, finger-snap, and other echolocation signals were explained to control participants and they were free to use the technique of their choosing, provided that the ‘signal’ was produced without any external device.

Stimuli

Four two-dimensional shapes were presented to all participants: a square (40 cm x 40 cm), a triangle[1] (52 cm x 45 cm [height]), a rectangle oriented horizontally (100 cm x 16 cm), and the same rectangle oriented vertically (see Figure 1A). All of the shapes were made of a 0.5-cm thick foam board and covered with aluminum foil. The shapes were positioned on a 0.6-cm diameter pole, which was determined to be undetectable by echolocation. Before beginning the experiment, all participants were familiarized with the four shapes (sighted controls were allowed only to touch the shapes and not to see them).

Procedure

All participants took part in two conditions: A 'free-moving' condition permitting head and body movements, and a 'fixed position' condition not permitting any movement. For both conditions participants EE1, EE2, and EE5 were tested in a Beltone Anechoic Chamber (18 feet high, 23 feet wide, 12 feet deep) at the National Centre for Audiology in London, Ontario, Canada. The chamber is equipped with a 125 Hz cut-off wedge system on the walls and ceiling, and ambient noise recordings indicated a noise floor of 18.6 dB (Larson-Davis System 824). Only participants EE1, EE2, and EE5 were tested in the anechoic chamber due to logistical reasons (i.e. additional participants were not available at the time of testing and the researchers had limited access to the chamber). For free-moving conditions, these participants were also tested in an echo-dampened room (2.75 m x 3 m, four walls covered in 3.8-cm convoluted foam sheets). After determining that there were no performance differences between the anechoic chamber and the echo-dampened room (see Results), we felt it was not necessary to test other participants in the anechoic environment. Therefore, all other participants in all conditions were tested in the echo-dampened room only.

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[1] Please note that the surface area of the triangle is slightly smaller than the other stimuli. This was done to make the triangle 'visually similar' in size to the other shapes. We had participants EE1-3 verify that this difference in surface area would not be informative regardless of shape. Furthermore, as also mentioned in the 'Results', we confirmed through analysis of error distributions that performance in 'triangle' conditions was the same as for the other shapes.

Table 1

Participant Details for Expert Echolocators (EE), Blind Controls (BC), and Blindfolded Sighted Controls (SC)

Group	Participant	Sex, Age	Cause of Blindness	Onset	Residual Vision	Echolocation Technique
EE	EE1	M, 45	Retinoblastoma	Early	None	Tongue-click
	EE2	M, 29	Glaucoma	Early, progressive	None	Tongue-click
	EE3	M, 56	Optic nerve atrophy	Early	None	Tongue-click
	EE4	M, 49	Retinoblastoma	Early	None	Speech, tongue-click
	EE5	M, 44	Retinopathy of prematurity	Early	None	Tongue-click
	EE6	F, 21	Idiopathic intracranial hypertension	Late	Bright light	Finger Snap
BC	BC1	M, 39	Leber congenital amaurosis	Early, progressive	Bright light	Speech, finger snap
	BC2	M, 34	Retinopathy of prematurity	Early	Bright light (left eye)	Finger snap, clap
	BC3	F, 25	Diabetes	Late	Low level vision (left eye)	Finger snap, clap
	BC4	F, 22	Glaucoma, cataracts	Early	Bright light	Speech, clap, finger snap
	BC5	M, 44	Retinopathy of prematurity	Early, progressive	Bright light	Speech, finger snap
	BC6	M, 20	Leber congenital amaurosis	Early, progressive	Bright light (left eye)	Finger snap
	BC7	M,40	Optic nerve atrophy	Early	None	Clap, finger snap
	BC8	F, 60	Retinoblastoma	Early	None	Speech, clap
	BC9	F, 24	Retinopathy of prematurity	Early	Bright light	Clap
	BC10	F, 32	Optic nerve atrophy	Early	Low level vision	Clap
SC	SC1	M, 30				Clap, speech
	SC2	M, 29				Clap, finger snap
	SC3	F, 22				Clap
	SC4	F, 58				Clap
	SC5	F, 31				Clap
	SC6	F, 45				Clap, finger snap
	SC7	F, 47				Clap
	SC8	F, 37				Clap
	SC9	F, 35				Clap
	SC10	F, 56				Clap, finger snap

On each trial, one of the four shapes was presented. The presentation height was unique for each participant in order to centre the shapes at ear-level. For the free-moving conditions (Figure 1B), participants were situated at a starting position 40 cm away (measured from the ears) and centered on the shape. Once the trial began, participants could freely move their heads and/or bodies to examine the objects via echolocation. For the fixed position condition (Figure 1C), participants were situated 80 cm away from the shape and had to keep their head and body still for the duration of the trial. This farther distance (compared to the 40 cm starting distance in the free-moving condition) was reported by three expert echolocators to provide the “best overall impression” of the shape. They mentioned that being any closer to the objects in the fixed position condition would prevent them from gathering object edge information from the echoes. The 80 cm position was used for the fixed position condition, then, to provide the best possible chance for successful performance in these cases. To validate the suggestion given by the expert echolocators, and to rule out distance as a confound, we conducted a control experiment which replicated the ‘fixed head’ conditions, but at a distance of 40 cm (Figure 1D). This experiment was conducted only with a subset of participants (EE3, EE6, SC2, SC3).

Throughout the experiment, participants used an echolocation technique of their choice (see Table 1) and listened for reflected echoes to determine the shape of the stimulus presented. For the fixed position condition, any participants who chose an echolocation technique other than mouth-clicks or other vocalizations were asked to keep the source of the sound (for example, their hand while finger-snapping) underneath the chin and as close to the body as possible and could not move from that position. For both conditions, participants were given a maximum of 15 seconds per trial and could provide their response at any point within that timeframe (4-alternative forced choice – ‘square’, ‘triangle’, ‘horizontal rectangle’, or ‘vertical rectangle’). For each trial the experimenter measured their response time (i.e. trial start until verbal response onset) using a stopwatch. For each condition, there were a total of 40 pseudo-random trials (10 repetitions per shape, per condition).

Results

For the purpose of the analyses, performance for each participant was collapsed across the four shapes (analyses not shown here revealed no significant differences in the individual shape response patterns for any of the groups). Therefore, the analyses were performed on the overall percentage correct value for each participant in each of the conditions (free-moving and fixed position). As mentioned in the Methods section, for the free-moving condition participants EE1, EE2, and EE5 were tested in both an anechoic chamber and an echo-dampened room. For each of these participants, we ran *t*-tests to determine if there were any performance differences between the anechoic chamber and the echo-dampened room. Results for all three participants revealed no significant differences in performance between the two rooms (EE1: *t*(78) = -5.30, *p* = .598; EE2: *t*(78) = 1.63, *p* = .107; EE5: *t*(78) =

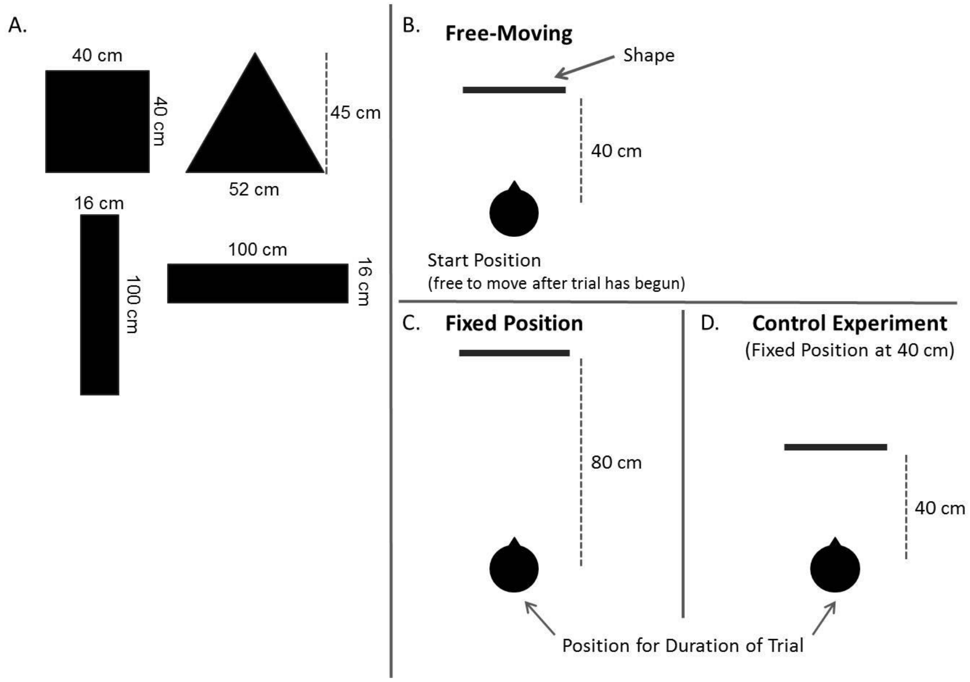

Figure 1. Stimuli and procedure for the free-moving and fixed position conditions. Four 2D shapes (A) were presented individually to participants. Shapes were made of foam board and covered in aluminum foil to maximize sound reflection. In the free-moving condition (B), participants were situated 40 cm away from the shape which was centered at ear-level. Once the trial began, participants could move freely in any direction (without touching the shape) in order to identify the shape via echolocation. In the fixed position condition (C), participants were situated 80 cm away from the shape and had to remain in that position for the duration of the trial without making any movements. We also ran a control experiment (D) on a subset of the participants to rule out the possibility of a distance confound between the free-moving and fixed position conditions. For all conditions, participants were given a maximum of 15 seconds per trial to identify the presented shape.

-1.113, *p* = .269). Therefore, for the purpose of the following analyses we averaged these participants' performance scores across the two testing environments.

A 3 x 2 mixed analysis of variance (ANOVA) was conducted on the data, with between subjects factor 'Group' and within subjects factor 'Condition'. The factor Group included three levels: expert echolocators (*n* = 6), blind controls (*n* = 10), and sighted blindfolded controls (*n* = 10). The factor Condition included two levels: free-moving and fixed position. Because there were fewer participants in the EE group and therefore there could be variability differences across groups, we computed Levene's tests for each condition. The results for both conditions were not significant (free-moving: $F(2,23) = 2.371$, $p = .116$; fixed position: $F(2,23) = 2.61$. $p = .095$).

The results of the ANOVA revealed a significant interaction between Condition and Group, $F(2,23) = 38.535$, $p < .0005$, $\eta^2 = .77$ (see Figure 2A). Bonferroni-corrected pairwise comparisons revealed that the EE group performed significantly better than both the blind ($p < .0005$) and blindfolded sighted ($p < .0005$) control groups in the free-moving condition. In the fixed position condition, the EE group also performed significantly better than both of the control groups (EE vs. BC: $p = .012$; EE vs. SC: $p = .043$), but this difference was substantially smaller (EE vs. BC: mean difference = 14.83; EE vs. SC: mean difference = 12.33). The drastic decline in the EE groups' performance in the fixed position condition is easily seen in Figure 2A, and pairwise comparisons reveal that the EE group performed significantly better in the free-moving condition ($p < .0005$). The performance of the two control groups in both conditions was statistically indistinguishable (free-moving: $p = 1$; fixed position: $p = 1$). Overall, the results of the interaction show that when the expert echolocators could freely moving their heads and bodies they had a substantial advantage and were able to reliably indicate the shape of the object presented to them. When they were required to remain still, however, their ability to indicate the shape of the objects decreased dramatically. Neither of the control groups showed this movement advantage.

To address the possibility that distance differences per se were responsible for the decrease in performance in the fixed position as compared to the free-moving condition, we had conducted a control experiment with a subset of participants. This control experiment replicated the fixed position condition, but at the 40 cm position. We used nonparametric related samples McNemar's tests to compare the individual participants' performance on fixed position conditions at each of the two distances. The results of this experiment are shown in Figure 2B. The data show that there was no advantage to being located at 40 cm in fixed position conditions. In fact, the EE participants' performance was the same (EE3: $p = 1$) or worse (EE6: $p = .008$) than their performance in 80 cm fixed position conditions. The sighted controls showed no significant difference in performance between the two distances (SC2: p = .5; SC3: p = .25). In sum, the difference in object distance between free-moving and fixed position conditions could not account for performance differences in the EE group.

Main effects of both Group and Condition were also found ($F(2,23) = 42.189$, $p < .0005$, $\eta^2 = .786$; $F(1,23) = 46.637$, $p < .0005$, $\eta^2 = .67$). Bonferroni-corrected pairwise comparisons for the main effect of Group revealed that the EE group performed significantly better than both of the control groups (EE vs. BC: $p < .0005$; EE vs. SC: $p < .0005$) but that the control groups performed identically (p = 1). Inspection of means showed that the main effect of Condition was due to the fact that, overall, participants performed significantly better in the free-moving condition as compared to the fixed position condition ($p < .0005$). This effect, of course, was driven by the high performance of the EE group in the free-moving condition, as was shown via the significant interaction.

To supplement the ANOVA analysis, we also ran individual t-tests on each group for each condition comparing performance to chance (25%) and the results were Bonferroni corrected for multiple comparisons. Performance was significantly different from chance only for the EE group in the free-moving condition, $t(5) = 8.013$, $p < .0005$. The EE group did not perform significantly better than chance when they were required to remain still ($t(5) = 2.019$, $p = .099$) and the BC and SC groups performed at chance level in both the free-moving and fixed position conditions (BC-free: $t(9) = .023$, $p = .982$, BC-fixed: $t(9) = -.943$, $p = .370$; SC-free: $t(9) = -.103$, $p = .920$), SC-fixed: $t(9) = .514$, $p = .619$). The results of the tests against chance are consistent with the ANOVA in that they provide support for a strong advantage for the EE groups in the free-moving condition.

Although the ANOVA allowed us to gain an understanding of the overall performance of the EE group compared to control subjects, it is important to appreciate that, similar to neuropsychological patients, blind echolocators show profound variability in their echolocation abilities as well as their

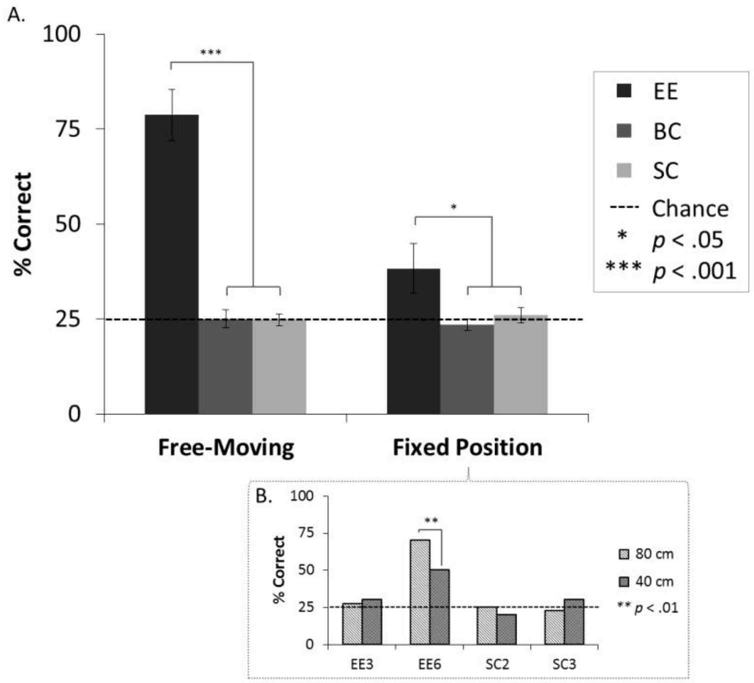

Figure 2. Percent correct performance of all groups (expert echolocators [EE], blind control [BC], sighted blindfolded controls [SC]) in each of the two conditions (free-moving and fixed position). Panel A presents the results of the omnibus ANOVA which revealed a significant interaction between the factors (significant differences indicated by asterisks). Error bars represent the standard error of the mean across participants and the dashed line indicates chance performance (25%). Panel B shows the performance of two expert echolocators and two sighted controls who were also tested at the 40 cm position in the fixed position condition. For reference we also show those participants' performance at 80 cm fixed position condition. It is clear from the data that being located closer to the objects in the fixed position condition provided no advantage. In fact, the echolocating participants showed comparable (EE3) or worse (EE6) performance at this distance (asterisks indicate a significant difference in performance at the two distances based on results from nonparametric related samples McNemar's tests). These data support our use of the 80 cm position in this condition which, according to the expert echolocators, provided the best overall impression of the shape and thus a better chance of successful performance.

history of use, cause and time of blindness, and so on. Therefore, we felt it was important to also analyze the data by treating each individual echolocator as a single case and comparing their performance in both of the conditions to the control participants. To increase statistical power for this analysis, and because the ANOVA revealed no significant differences in performance between the control groups, we combined the control groups for each condition (free-moving and fixed position) for the purpose of this analysis. For each EE participant, we ran modified *t*-tests to compare their performance to that of the combined control group for both conditions (see Crawford & Garthwaite, 2002; Crawford & Garthwaite, 2007; Crawford & Garthwaite, 2012; Crawford, Garthwaite, & Porter, 2010; Crawford & Howell, 1998). The modified *t*-test is an extension of the traditional *t*-test but has been adapted to compare a single case to a control group. For the free-moving condition, the results of the modified *t*-tests revealed that each individual echolocating participant performed significantly better than the combined control group (see Table 2 for all *t*- and *p*-values and Figure 3A for a graphical depiction of each individual's performance against the control group). The effect size of each echolocator's score also reveals that they reliably performed well above the level of the control group (see Figure 3B). In the fixed position condition, however, only participants EE2, EE4, and EE6 performed significantly better than the control group, and the effect size of the difference in performance was substantially lower than in the free-moving condition (with the exception of EE6 who showed high performance in both conditions; see Figure 3).

We also ran a 3 (Group) x 2 (Condition) mixed ANOVA on the participants' response times, but this analysis did not reveal any significant results (Condition x Group: $F(2, 23) = .524$, $p = .599$, $\eta^2 = .044$; Condition: $F(1, 23) = 4.14$, $p = .054$, $\eta^2 = .153$; Group: $F(2,23) = 2.995$, $p = .07$, $\eta^2 = .207$). There was a trend toward significance for the main effect of Condition, suggesting that, overall, participants used slightly more time in the free-moving condition, but Bonferroni-corrected pairwise comparisons did not reveal a significant difference.

Overall, the results show that expert echolocators can consistently and reliably indicate the shape of 2D objects when they are allowed to make head and body movements while echolocating. When they are required to remain still, however, performance drops to a level that is statistically indistinguishable from chance. In fact, our single-case analysis shows that in free-moving conditions all our experts perform statistically superior to the control group, whereas only half of them perform superior in fixed conditions. Neither blind nor sighted blindfolded controls showed a movement advantage in the free-

Table 2.

Results of Modified t-test Analysis Comparing Individual Echolocators to Non-echolocating Controls

Free-Moving							**Fixed Position**						
Control Sample					Significance Test		Control Sample					Significance Test	
n	**Mean**	**SD**	**Case**	**Score**	***t***	***p***	***n***	**Mean**	**SD**	**Case**	**Score**	***t***	***p***
20	24.94	6.3	EE1	77.5	8.14	.000	20	24.75	5.61	EE1	27.5	.478	.319
			EE2	86.25	9.495	.000				EE2	37.5	2.217	.019
			EE3	85	9.302	.000				EE3	27.5	.478	.319
			EE4	77.5	8.14	.000				EE4	37.5	2.217	.019
			EE5	48.75	3.687	.000				EE5	30	.913	.186
			EE6	97.5	11.238	.000				EE6	70	7.866	.000

Note. Means (control groups only) and case scores are percentage values (percent correct performance). Significance values (*p*) are one-tailed.

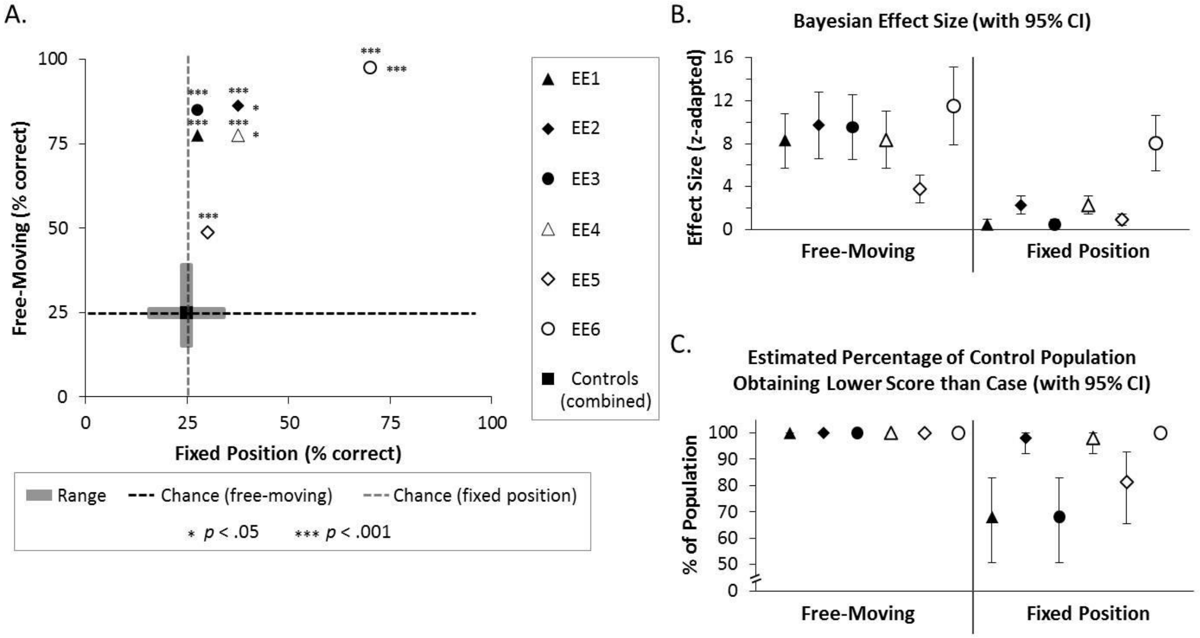

Figure 3. Results of the individual case analyses for the free-moving and fixed position conditions. Each individual echolocator's performance in the free-moving (y-axis) and fixed position (x-axis) conditions are shown in Panel A. The data from the combined control group is also shown, with the shaded bars in each direction indicating the range of scores for each condition. Significant results from the modified *t*-tests are indicated by asterisks. Asterisks above a data point indicate a significant difference from the combined control group in the free-moving condition, and asterisks to the right of a data point indicate a significant difference from the combined control group in the fixed position condition (see Table 2 for results from all individual tests). Dashed lines in each direction represent chance performance. The

Bayesian effect size (with error bars showing 95% confidence intervals (CIs); in some cases CIs are so small that error bars are not visible) for the results of each individual *t*-test are shown in Panel B. The effect size was calculated using adapted *z* scores (Crawford et al., 2010). The 'abnormality' of the case's scores are presented in Panel C which shows the percentage of the control population (with 95% CIs) that would obtain a lower score than the case. The information presented here and in Table 2 fully meet the reporting standards set out by Crawford et al. (2010).

moving condition; in fact, their performance was nearly identical in each of the conditions and never deviated from chance.

Discussion

The aim of the current experiments was to determine if (1) blind expert echolocators can determine the 2D shape of objects by analyzing the echoes reflected from the edges of similar objects, and (2) if movements of the head and body while echolocating are crucial for successful shape identification in our task. The results were clear. Expert echolocators were exceptional at determining the shape of objects that differ only in their edge or contour properties, and they performed well above blind participants who do not echolocate and sighted participants who were blindfolded. When the echolocators were required to remain still, however, performance fell substantially, and was statistically indistinguishable from chancel level. Therefore, our results show that blind expert echolocators can use echoes to successfully determine the shape of similar objects, and this ability is critically dependent on the use of head movements. In our study echolocators could move freely, which means that they could perform both angular movements as well as movements in depth. Future research should aim to investigate the relative contributions of these separate aspects of head motion in more detail.

As mentioned in the Methods, blind and sighted control participants did not receive any explicit echolocation training prior to participation. Not surprisingly then, these participants were unable to successfully use echoes to discern the shape of the objects. This runs contrary to the findings of Hausfeld et al. (1982) who found that untrained sighted participants could identify simple shapes using echoes. Although these participants were untrained, they received feedback on every trial and improvements in performance over the first few trials indicates that this feedback was useful. In fact, the participants in their study reported that during the initial trials they were simply memorizing which echo was associated with which shape, and then applied this knowledge to the remaining trials. It is unclear, then, whether the participants were actually perceiving object shape or were simply relying on subtle differences in echo characteristics without perceiving any shape details. Therefore, the role of feedback, and other methodological differences, may explain the differences in performance between untrained participants in the current study and in Hausfeld et al.'s experiments.

An important consideration in the design of the experiment is the fact that the distance at which the shape was presented was different for the free-moving and fixed position conditions. Therefore, one could argue that the difference in distance alone may underlie the EE group's decrease in performance in the fixed position condition. We addressed this in our control experiment, and the results of that experiment (see Figure 2B) suggest that distance per se cannot explain performance differences between free-moving and fixed conditions. Furthermore, if it were the case that distance per se could account for performance differences between free-moving and fixed position conditions, we would expect a similar distance effect for all groups, but this was not the case. Finally, we want to highlight once more that the farther position for the fixed position condition was chosen based on echolocators' advice because they found that this distance gave them a better impression of shape as compared to closer distances. This can be understood considering that if an individual is situated very closely to an object and required to remain still, the majority of the echolocation signal will be reflected from the center of the object, thus lacking edge information that could be used to discern the object's shape. One can imagine a similar situation in vision when an individual is situated very close to an object and is unable to gather information about object features in the periphery without movements of the head and/or eyes. This problem could be solved by simply moving farther away from the object.

A final thing to consider is that more people in the blind control group reported having some residual vision than the expert echolocators (Table 1). It is possible that the presence of some residual vision in a blind individual might make them less inclined to develop echolocation as a strategy. But this need not always be the case. Participant EE6, for example, had some residual vision at the time of testing but even so had mastered echolocation and performed better on the task than any of the other expert echolocators. In any case, it seems unlikely that the degree of vision normally available determines how well people can use echoes to discriminate shape. After all, the blind controls did not perform better than the sighted controls when both groups were blindfolded. Furthermore, the two totally blind individuals (BC7, BC8) in the blind control group performed no better or worse than the rest of that control group, again suggesting that it was expertise per se and not degree of blindness that drove performance in our study.

In sum, our results show that blind expert echolocators can use echoes to successfully determine the shape of similar objects, and this ability is critically dependent on the use of head movements.

Head movements made while echolocating may be similar to the multiple eye movements, or saccades, a sighted person makes when visually scanning a large object or a scene. These saccades allow a person to accumulate visual information from the boundaries of a large object and the features of a visual scene, which are then pieced together to create an overall perceptual representation. This process, termed transsaccadic integration, requires the brain to make quick computations of the incoming visual information in order to arrive at a rich and stable representation of an object or scene (Neimeier, Crawford, & Tweed, 2003; Prime, Vesia, & Crawford, 2011). In terms of echolocation in the current study, making head movements while producing mouth-clicks (or other signals) could have provided sound snapshots – or ‘echo saccades’ – that are then automatically pieced together by the brain to provide the individual with a perceptual representation of the object. While transsaccadic integration in vision can occur in a few hundred milliseconds, human echolocation is by comparison much more time-consuming and effortful. Furthermore, the resulting percepts are likely coarser than in vision. In fact, it has been recently shown that the precision of echolocation is comparable to visual acuity in the periphery, which, when compared to foveal acuity, is quite poor (Teng et al., 2011).

Further evidence to support our suggestion that the head movements made by echolocating humans might serve a similar function as visual saccades comes from a recent study on scanning movements in echolocating bats (Seibert, Koblitz, Denzinger, & Schnitzler, 2013). It was suggested that each bat signal-echo pair was comparable to a visual fixation and that the movements made by the bat between signal-echo pairs are comparable to visual saccades. The researchers found that the bats' scanning behaviours changed depending on the environment they were in and the task they were performing. In particular, when the bats were examining a scene they made large scanning movements but when they detected an object or obstacle the angle of the movements was much smaller. This is quite similar to vision in that the pattern of head and eye movements can be quite different based on if one is looking at a large visual scene – which requires larger, longer movements – or looking at an object within a visual scene – which requires smaller, shorter movements to gain greater object-specific detail (Hardiess, Gillner, & Mallot, 2003; Rayner, 1998). Considering these findings in echolocating bats and our results showing the advantage of using head movements in human echolocation, it is important for future research to address the different types of movements made by expert echolocators and how these movements change in different environments and tasks.

Although it is quite clear that head movements – or 'echo saccades' – seem to facilitate 2D shape perception in echolocation, one of our echolocating participants, EE6, showed impressive performance in both of the conditions. An important consideration is the fact that EE6 used a finger-snap as opposed to the tongue-click signal used by the other echolocating participants. As mentioned in the Methods section, any participants who used a signal other than tongue-clicks or other vocalizations had to keep the source of the signal (in this case, the hand) close to the body, under the chin, and as still as possible. It is possible, however, that slight movements were made that were not noticed by the researcher and possibly not even by the participant herself, and that these might have aided performance. One might also consider the choice of signal *per se* aiding performance, i.e. EE6 used a finger snap whereas the other EEs used tongue clicks. Yet, several of the control participants used finger snaps as well, without the advantage we saw in EE6.

In addition to being potentially relevant for explaining EE6's impressive performance, the question of the choice of signal is also relevant for the current study because the majority of control participants used a signal that was different from the echolocating participants (with the exception of EE6). Nevertheless, it is important to note that, even though the majority of our EE participants used mouth-clicks, this is not to say that they use this type of signal exclusively in everyday life. In fact, almost all of the echolocators report using claps, finger-snaps, and other techniques. So, the variety of signals used by echolocators in real life – and the various signals used by participants in the current study – raises an important question: what is the best signal to use for echolocation? This question has been addressed previously (Rojas, Hermosilla, Montero, & Espi, 2009; 2010) but a consensus is lacking. For example, longer signals (500 ms) may be better than shorter ones because they result in a surplus of echo information due to repetition pitch (Schenkman & Nilsson, 2010). Also, it has been suggested that noise signals provide more and better information than click signals (Arias & Ramos, 1997), though it has also been suggested that in particular the palatal tongue click is the best signal for echolocation (Rojas et al., 2009). Therefore, it is unclear whether participants' choice of signal in the current study could have directly affected performance (regardless of movement) because there is no clear indication of what is the best echolocation signal. Also, it is important to note that most systematic studies of the signals used in echolocation (and many studies on echolocation in general) use artificial sounds played by a loudspeaker or through headphones. Therefore, it is important for future research to address the use of self-produced signals in order to better understand the use of natural, active echolocation and maximize the information content of echoes.

It can be argued that, at a basic level, the ability to echolocate involves some combination of increased echo sensitivity (Dufour, Després, & Candas, 2005; Kolarik, Cirstea, & Pardhan, 2013), suppression of the precedence effect (Wallmeier, Gebele, & Wiegrebe, 2013), and, of course, intact hearing (Schenkman & Nilsson, 2010). This is encouraging because it means that the ability to echolocate is available to all people, blind or sighted. Therefore, we believe that the use of echolocation should be more actively promoted in the blind community because, even if one learns to echolocate only at a very basic level, it would provide another resource for perceiving one's surroundings and gaining further independence in life. In fact, a recent survey has shown that the use of echolocation by the blind may have real-world advantages (Thaler, 2013). In particular, blind echolocators have higher salaries and greater mobility in unfamiliar places than blind individuals who do not echolocate. Of course, other variables likely mediate these advantages, but even the additional information that an echolocator possesses about his surroundings – which then aid in obstacle avoidance, navigation, and object perception – is an advantage in itself.

Overall, the results of the current experiments show that active echolocation is a useful resource that allows blind individuals to gather accurate object shape information from faint echoes. Even this basic application of echolocation shows how useful it can be, by providing blind individuals with perceptual information that they would otherwise not have access to. Considering echolocation is a trainable skill, there is great potential to offer valuable and liberating opportunities for the blind and visually-impaired.

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